The tall cells pictured in Fig. 1 form the lining of the small intestine in humans and other animals. These cells spend their lives secreting digestive enzymes and absorbing the broken-down food molecules. Intestinal cells like this need to be replaced often, usually every 3-6 days. As a result, these cells tend to reproduce themselves frequently.

Reproduction is one of the characteristics that all living things share, but the type of reproduction we are discussing here is cellular reproduction, the process of making more cells. This isn't necessarily the same thing as an organism's reproduction, where whole organisms make offspring. Only single-celled organisms reproduce themselves by cellular reproduction (Table 1). Multicellular organisms, such as ourselves, have more elaborate ways to reproduce ourselves. We still have use for cellular reproduction, however.

<table>
<thead>
<tr>
<th>Type of organism</th>
<th>Use for cellular reproduction</th>
<th>Example</th>
</tr>
</thead>
<tbody>
<tr>
<td>single-celled</td>
<td>organismal reproduction</td>
<td>Bacteria contaminating leftovers in refrigerator</td>
</tr>
<tr>
<td>multicellular</td>
<td>increasing cell numbers (growth) and tissue repair/regeneration</td>
<td>Bone lengthening during adolescence; an oak tree healing tissue wounded by chainsaw</td>
</tr>
</tbody>
</table>

The life of a cell can be summarized with a figure that we refer to as the cell cycle (Fig. 2). The cell cycle shows us many of the significant events of a cell's life from the moment it is born until it reproduces.
Interphase

The term *interphase* refers to the period between cell divisions (*inter-* = between). For the vast majority of cells, cell division represents only a small fraction of their lives. Therefore, cells spend most of their lives in interphase.

Interphase is divided into three subphases: G\textsubscript{1}, S, and G\textsubscript{2}. The G\textsubscript{1} and G\textsubscript{2} phases are sometimes called *gap phases*. S phase refers to DNA synthesis, when the cell copies its DNA prior to division.

\[ \text{Fig. 2. The eukaryotic cell cycle is divided into phases.} \]

How do cells “know” when to proceed out of G\textsubscript{1} and into S phase?

Cells usually respond to cues from other cells. These cues can come in the form of attachments to their neighbors or molecules (called *growth factors*) that bind to receptors on the cell’s surface.

If you use the example of the intestinal cells on the previous page, imagine that one of those cells is scraped off by food or killed by acid. The cells on either side would detect the damaged cell and would begin preparations to divide and fill in the gap.

Normally, cells will not advance out of G\textsubscript{1} unless they receive such a signal. This type of control is necessary so that cells don’t divide uncontrollably.

S Phase

Cells that are committed to dividing exit G\textsubscript{1} and enter S phase. In order for the daughter cells to function properly, they need a full complement of the mother cell’s DNA. Therefore, the mother cell must completely copy her DNA so that she has one copy for each daughter.

The DNA within the nucleus is organized into several chromosomes, the number of which is specific to the organism’s species. Most human cells carry 46 chromosomes, but chromosome numbers in other species can vary from as few as 4 (the flowering plant *Haplopappus*) to as many as 308 (the black mulberry tree). Chromosomes are composed of chromatin, a long strand of DNA wound around a class of scaffolding proteins called histones.

Chromosome terminology can be confusing. An unreplicated chromosome is a single piece of DNA with a central structure called a centromere (usually near the middle of the chromosome; Fig. 3). When the DNA is copied, the original and the newly-created copy are held together at their centromeres. Each piece of DNA is called a sister chromatid. This is similar to photocopying a sheet of paper and stapling the original and the copy together (each sheet is a sister chromatid). During a later event in the cell cycle, the two sheets will become “unstapled” and separated. Following separation, each sister chromatid is now considered a full-fledged chromosome.
G₂ Phase
In G₂, cells make their final preparations for division. This usually involves growing in size and making more copies of their organelles. For instance, let’s say that a cell needs a minimum of 100 mitochondria to survive. If the mother cell has 100 and it divides, each daughter will only have 50. Therefore, the mother cell needs to bulk up its mitochondria before dividing so each daughter cell has a decent chance of survival.

Cell Division: M Phase (Mitosis and Cytokinesis)
Once the preparation during interphase is complete, the cell progresses into the mitotic (M) phase. During the mitotic phase, the cell accomplishes two important tasks:

- Sister chromatids are separated from each other, often referred to as nuclear division.
- The cytoplasm and organelles are separated and partitioned into two new daughter cells. This is referred to as cytoplasmic division.

Nuclear division occurs in a process called mitosis. Once the sister chromatids have been segregated to new nuclei, the cytoplasm is split during cytokinesis.

Mitosis
The following two pages summarize the four phases of mitosis: prophase, metaphase, anaphase, and telophase (Fig. 4a and 4b). Mitosis is like a ballet starring chromosomes. They change in appearance, they move out into the cytoplasm, they line up, they move away from each other, and they find new homes. The dynamic nature of mitosis is partly due to their association with microtubules, members of the cell’s cytoskeleton. We have already observed their dynamic nature in class; now we can see them in action.

One important note: the phases of mitosis are man-made inventions for our convenience. In reality, one phase tends to “melt” into another and it can be difficult to visualize boundaries between the phases when observing live cells.
By the end of interphase, the cell is prepared to divide. It has reached an appropriate size and has increased the number of its organelles.

Additionally, the DNA has been replicated and each chromosome contains two sister chromatids held together at its centromere.

Look at the stained interphase cell at the top of the page. The DNA is stained blue with a fluorescent dye. During interphase, the chromatin that makes up the chromosomes is loose and unwound. This means that it is not possible to see individual chromosomes.

Pro- means “before.”

Prophase sets the stage for the separation of the chromosomes. Three significant events occur in prophase:

1. The centrosomes begin to move towards opposite poles of the cell. Centrosomes are structures in the cytoplasm of the cell that produce protein fibers called microtubules. As the centrosomes move away from each other in opposite directions, the microtubule “web” they produce (called the mitotic spindle) spans across the cytoplasm;

2. the chromatin begins to coil and condense, and now individual chromosomes can be seen (see the two prophase micrographs above); and

3. the nuclear envelope begins to break down, leaving the chromosomes in the cytoplasm.
**Fig. 4b. The Cell Cycle: Metaphase, Anaphase, and Telophase**

**Metaphase**

Meta- means “across.”

In metaphase, the chromosomes have all become attached to the spindle at their centromeres.

The spindle pulls and pushes the chromosomes until they are equally spaced between the centrosomes. This gives the appearance that they are lined up along the middle of the cell. The imaginary line along which they are arranged is called the **metaphase plate**. The metaphase plate is generally across the middle of the cell, but there can be exceptions to this.

**Anaphase**

Ana- means “back.”

Once the chromosomes are lined up, two events occur in rapid succession.

First, the centromeres separate and the two sister chromatids are no longer attached to each other.

Second, the microtubules of the spindle dramatically shorten, pulling the sister chromatids away from each other and towards opposite poles of the cell.

Once the sister chromatids separate, they are each considered full-fledged daughter chromosomes.

**Telophase and Cytokinesis**

Telo- means “end.”

Telophase is, in many ways, like prophase run in reverse.

Once the new chromosomes reach the poles, new nuclear envelopes will reform around them. Inside each new nucleus, the chromatin will relax and the individual chromosomes will no longer be visible.

Telophase happens simultaneously with cytokinesis, the physical separation of the cytoplasm. Cytokinesis will be discussed next.
Cytokinesis

Once mitosis is complete and the new daughter nuclei have formed, the cytoplasm will be separated into two daughter cells. This process is called cytokinesis (cyto- = cell; kinesis = movement). In eukaryotes, there are two ways that cytokinesis can occur, depending on the presence or absence of a cell wall.

In animal cells (which lack cell walls), the mother cell literally pinches off into two daughter cells in a process called cleavage (Fig. 5a). Cleavage is accomplished by actin filaments beneath the plasma membrane. These actin filaments are arranged in a ring that encircles the inside of the cell. During cleavage, this ring contracts, getting smaller and smaller. The effect is like a drawstring closing a bag. As seen from the outside, a deep furrow (called a cleavage furrow) appears to slice the cell in half. Eventually, the mother cell is pinched into two daughter cells.

![Cytokinesis](a) Cleavage of an animal cell (SEM)

![Cell plate formation](b) Cell plate formation in a plant cell (TEM)

*Fig. 5. Cytokinesis is performed differently in (a) animal cells vs. (b) plant cells.*

Plant cells are surrounded by rigid cell walls and cannot pinch as animal cells do. Rather, plant cells separate themselves by constructing a new cell wall between the two nuclei (Fig. 5b). Vesicles containing cell wall material line up between the daughter nuclei and fuse together. The cell wall material inside the vesicles forms a structure called a cell plate which eventually grows into the new cell wall.
Important points to remember

• Cells spend the majority of their lives in G\textsubscript{1} of interphase, performing their specific cellular functions. They will only proceed towards division if called upon.

• During S phase, the cell replicates all of its DNA. This is to ensure that both daughter cells receive a full complement of genes.

• Before DNA replication, a chromosome looks like this:

![Centromere](image1)

• Following DNA replication, the original DNA and its copy are held together by their centromeres. A duplicated chromosome looks like this:

![Two sister chromatids](image2)

• Sister chromatids are exact copies of each other, generated during DNA replication.

• Cell division occurs in two general steps:

  - \textit{mitosis}, which is separation of the chromosomes (nuclear division); and
  - \textit{cytokinesis}, which is separation of the cytoplasm (cytoplasmic division).

• The products of cell division are two daughter cells that are exact copies (clones) of each other. They are also identical to the mother cell that created them.